

# THE ROLE OF NECTAR ROBBERS AND POLLINATORS IN THE REPRODUCTION OF *ERYTHRINA LEPTORHIZA*<sup>1</sup>

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## ABSTRACT

The pollination ecology of *Erythrina leptorhiza* is discussed. Flowering takes place synchronously during the rainy season. The species is self-incompatible and produces some flowers with short styles. The flowers are adapted for hummingbird pollination in their morphology and high nectar production early in the day. Of four bird visitors, three were nectar robbers (89% of the total foraging visits) and one was a legitimate, traplining pollinator (11% of the foraging visits).

All species of the genus *Erythrina* are bird pollinated (Raven, 1974, 1977; Toledo, 1974). Although most American species are pollinated by hummingbirds (Toledo, 1974), there are reports of nonspecialized passerine birds visiting *Erythrina* on this continent (Skutch, 1954; Timkin, 1970; Snow & Snow, 1971; Leck, 1974; Raven, 1974; Cruden & Toledo, 1977; Toledo & Hernández, this symposium). Although there are numerous observations about hummingbirds visiting species of *Erythrina* (see Toledo, 1974: table 1), detailed studies of pollination by hummingbirds in this genus have been initiated only recently (Toledo, 1974; and many others). The present study of *E. leptorhiza* A. DC. was made because of our ignorance of its pollination ecology, and because it shares characteristics of both perching- and hummingbird-pollinated species. As pointed out by Krukoff & Barneby (1974: 362), it shows affinity with the sympatric *E. breviflora* A. DC. (perching bird-pollinated, Cruden & Toledo, 1977) in habitat, pod and seeds. Furthermore, "the very high amounts of amino acids in many samples of seeds of *E. leptorhiza* suggest affinities with species of sect. *Breviflorae* and *Edules*" (Romeo, 1973: 65; quoted by Krukoff & Barneby, 1974: 363). In this paper an account is given of the pollination ecology of *E. leptorhiza*, and the role played by its visitors is discussed in the light of flowering phenology, flower characteristics, and breeding system.

## STUDY AREA AND METHODS

*Erythrina leptorhiza* is endemic to temperate elevations ( $\pm 1,800$ – $2,700$  m) in southcentral Mexico, ranging from the southern edge of the Central Plateau through the Transverse Volcanic Range to Puebla (Krukoff & Barneby, 1974: 362). It is characterized by its herbaceous habit of growth and is usually found in a secondary succession in the oak and pine-oak forest. This perennial herb

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has the ability to reproduce itself vegetatively by rhizomes. The individual plants die back to soil level each year before the dry winter season and grow in the following wet season to become reproductive by seed again.

Our field observations were made primarily in a deciduous forest situated 51 km SE of Mexico City, Morelos, on the road between Xochimilco and Oaxtepec, during June and July 1978. The site is noted for the high number of *Erythrina leptorhiza* plants, probably as a result of fire in this part of the forest.

For a quantitative evaluation of flowering and setting of the fruit, we made some counts on 25 randomly selected plants at regular intervals. Nectar volumes were measured with calibrated micropipets ( $10\ \mu\text{l}$ ) from freshly opened flowers, before the nectar had time to become more concentrated by evaporation and before it could be removed by floral visitors. At the same time, we measured the sugar concentration with an Erma Hand Refractometer, model A. Presence of floral dimorphism was determined by style and stamen measurements for several individual plants. Measurements were made in the laboratory on previously fixed flowers in anthesis. The size of ovules and pollen grains was determined by microscopic examination and measurements. Controlled artificial pollination experiments employing the techniques of Bawa (1974) were carried out to test for self-compatibility.

#### FLOWERING PHENOLOGY AND FRUIT SET

Like *Erythrina breviflora* (Cruden & Toledo, 1977), *E. leptorhiza* flowers during the rainy season and is leafy at anthesis, in contrast to the flowering strategy of many other Mexican species of *Erythrina*. Field observations indicates that almost all the individuals begin to flower synchronously as early as mid-May, ending in the second half of August. This is in accordance with data on herbarium sheets.

Figure 1 shows a partial account of flowering dynamics. The solid line indicates the number of opened flowers, and the broken line indicates the fruit set (percent of flowers that develop into fruit). It is important to mention that fruit set was calculated independently for three different periods of time (see Fig. 1). Thus, fruit production begins almost at the final phase of flowering. Then, its rate of production increases. In other words, fruit set is increasing while the number of available flowers decreases.

#### INFLORESCENCE, FLORAL MORPHOLOGY, AND NECTAR PRODUCTION

Contrasted with the species which flower during the dry season and have compact racemes, the inflorescence of *Erythrina leptorhiza* is an elongated raceme (Fig. 2A). The flower stalks usually grow singly and each has an accompanying branch of leaves. Each inflorescence has from 24 to 60 or more flowers. Its floral structure is quite similar to that of all hummingbird-pollinated species of *Erythrina*. The narrow standard is orange and encloses the sexual organs. The stamens are in four levels as they are of different lengths, thus enlarging the contact's surface with the visitor. The anthers face upwards facilitating deposition of pollen



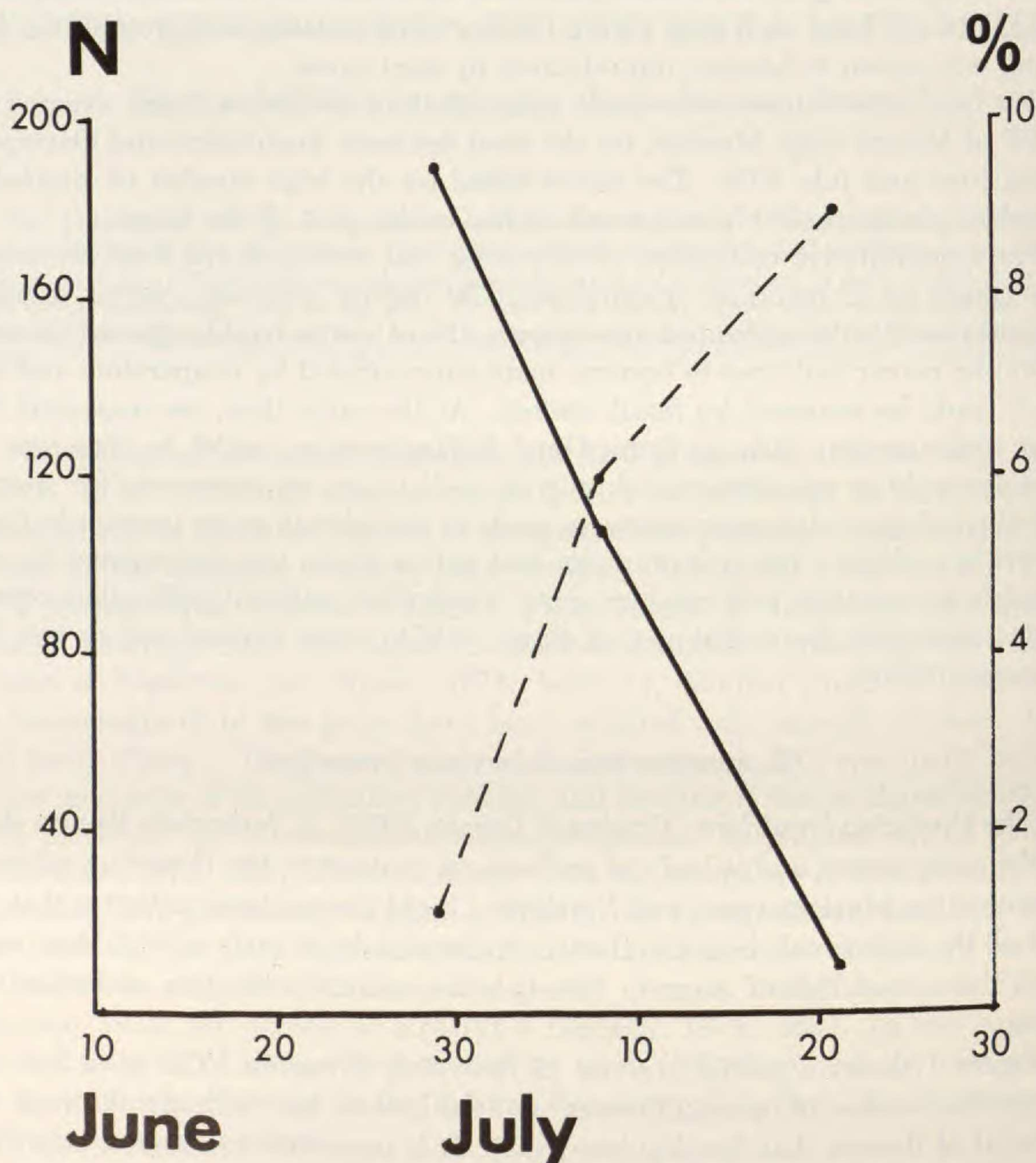


FIGURE 1. Final phase of flowering and setting of fruit of *Erythrina leptorhiza*. N = solid line = number of opened flowers; % = broken line = percent of flowers that develop into fruit.

on the throat or bill of the hummingbird. The pistil lies in the center of the stamens. Several characteristics of the flower seem to be very variable. Thus, the corolla color varies from pale to bright orange in flowers at anthesis. Both calyx and corolla are quite variable as well, with ranges of 27–39 mm and 65–87 mm respectively. The size of the longest stamen ranges from approximately 51 to 74 mm.

The daily pattern of nectar production of *Erythrina leptorhiza* is similar to many hummingbird-pollinated species of plants. Thus, there is a very high nectar production in the early morning [42.5 (33–50  $\mu$ l)]<sup>3</sup>, then a rapid decline to low levels by afternoon. The sugar density is 22.7%, ranging from 21.7% to 23.5%.



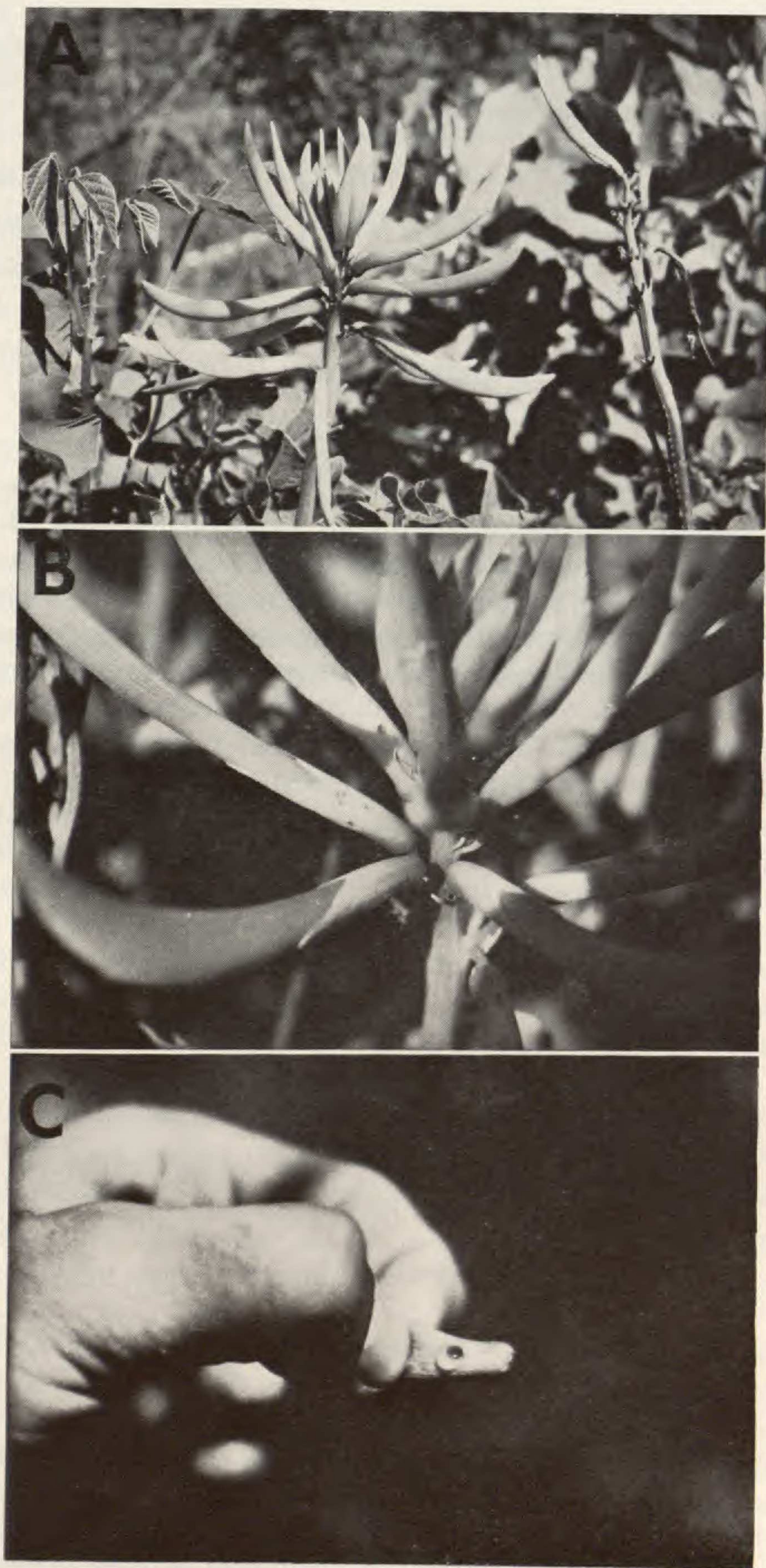


FIGURE 2. *Erythrina leptorhiza*.—A. Inflorescence.—B. Detail of inflorescence showing the holes made by *Diglossa baritula* on the calyx.—C. Perforate calyx with a drop of nectar.



TABLE 1. Morphology of the floral forms in *Erythrina leptorhiza*.

	Long Styles	Short Styles
Style length (mm) <sup>a</sup>	58 (48–69)	23 (18–35)
Number of ovules <sup>a</sup>	7.4 (3–10)	10.6 (7–12)
Ovule size (μ) <sup>b</sup>	893.5 × 728.5	602.8 × 480.4
Pollen grain size (μ) <sup>b</sup>	31.7 × 27.5	27.5 × 24.7

<sup>a</sup> Mean and range.<sup>b</sup> Mean.

## BREEDING SYSTEM

In our population we found two types of flowers: (1) with long styles; and (2) with short styles. The stamen lengths are the same in both kinds of flowers ( $\bar{x}$  = 61 mm in the longest stamen), although there is dimorphism in other floral parameters (Table 1). In the long-styled flowers the anthers are just in front of the stigma, while in the short-styled ones the stigma does not come in contact with the anthers. In these there is a dimorphism in both ovule and pollen grain sizes, and the average number of ovules is different as well. In short-styled flowers the styles are incurved at the tip, through 90°, so the stigma is oriented toward the standard. By contrast, those of the long-styled flowers are completely straight.

The long-style flowers constituted 82.8% of our sample (N = 64), the remainder being of the short-style flowers. Nevertheless, we do not know the real proportion of each flower form in the population.

Investigation of the breeding system indicates self-incompatibility in *Erythrina leptorhiza*. We found two cleistogamic flowers on a long-styled plant. These flowers with nondeveloped corollas were able to produce fruit.

## VISITORS: NECTAR ROBBERS AND POLLINATORS

We were able to identify four species of birds visiting the flowers of *Erythrina leptorhiza* (Table 2). These birds fall into two groups: the nectar robbers that take the nectar by illegitimate foraging, and the pollinators. The Mexican flowerpiercer (*Diglossa baritula*) was observed robbing the nectar by perforation of the calyx (Fig. 3A). The functioning of the mandibular mechanism of *Diglossa* during the process of perforation and feeding has been described by Lyon & Chadek (1971). Apparently, perforation of *E. leptorhiza* flowers by *D. baritula* is very easy, probably because of the thin-chartaceous texture of the calyx. The high percentage of opened flowers with holes (91.5, 100, and 100% in three different counts) reflects the preference of this nectarivorous bird for the flowers of *E. leptorhiza* (Figs. 2B–2C). In the same group fall two species of hummingbirds of moderate size: *Amazilia beryllina* and *Hylocharis leucotis*. The approach of these hummingbirds to the flowers of *E. leptorhiza* is quite different from that

<sup>3</sup> Mean and range (μl).



TABLE 2. Number of foraging visits recorded for species of birds visiting flowers of *Erythrina leptorhiza*.

Species	Date and Length of Observation		
	16/VI/78 (1 h)	29/VI/78 (6 h)	8/VII/78 (3½ h)
<i>Amazilia beryllina</i>	4 <sup>2</sup>	18	4
<i>Hylocharis leucotis</i>	—	7	11
<i>Lampornis clemenciae</i>	1	3	3
<i>Diglossa baritula</i>	—	5	7

generally observed in most *Erythrina* species (Toledo, 1974). They take the nectar by plunging the beak into the calyx, but from the external side of the standard (Fig. 3B). As the hummingbird's beak does not enter into contact with the anthers, obviously there is no effective pollination. The degree of mutual aggressiveness between hummingbirds and *D. baritula* is considerably less than among different hummingbirds and conspecifics. In most cases hummingbirds and *D. baritula* ignore each other; nevertheless, we observed some threat displays of the flower-piercer towards *A. beryllina*.

The large blue-throated hummingbird (*Lampornis clemenciae*) is the one species that exploits the nectar in a legitimate way. Contrasted with the above-described style of hummingbird visitation, this species goes into the calyx, where the nectar is deposited, from the inner side of the standard (Fig. 3C). The bird's head remains a short time between stamens and standard, and, as a consequence, its bill and throat become coated with pollen. The "trapline" was the general feeding strategy of *L. clemenciae*. Birds of this species travelled between clumps of flowers following a regular route. We checked on the fruit production in a place where *L. clemenciae* was a systematic visitor, and it was higher than elsewhere in the area (fruit set = 16.14).

Lucifer hummingbird (*Calothorax lucifer*) was a common visitor of *Fuchsia microphyla* H.B.K. and other ornithophilous flowers of the forest but was never seen drinking the nectar of *Erythrina leptorhiza*. Hummingbirds usually utilized alternative nectar sources, e.g., *Bouvardia ternifolia* (Cav.) Schlecht., *Calliandra grandiflora* (L'Her.) Benth., *Castilleja canescens* Benth., *Penstemon campanulatus* Willd., *Psittacanthus schiedeana* (Schlecht. & Cham.) Blume ex Schult., and *Spiranthes aurantiaca* (Llave & Lex.) Hemsley.

## DISCUSSION

The results obtained from the observations are very suggestive. It is possible to limit the discussion to the following three aspects: (1) the variability of the flowers, (2) the role played by the flower visitors in the breeding behavior of *Erythrina leptorhiza*, and (3) the relationship between flower dynamics and fruit set.

The floral structure of *Erythrina leptorhiza* is quite variable. Flowers with short styles are distinct in the orientation of the stigma, number of ovules, and



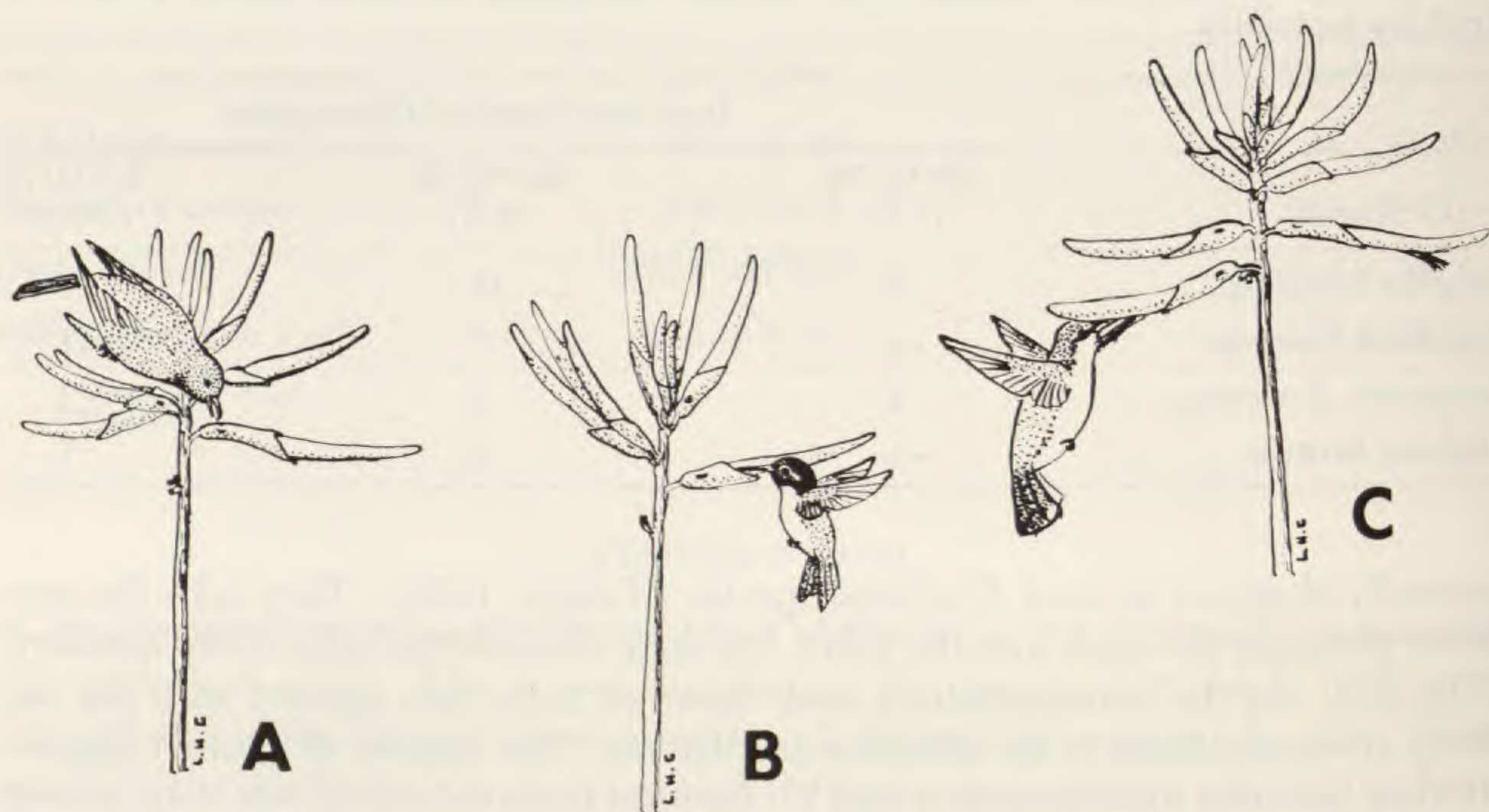


FIGURE 3. The three modalities of bird visitation to the flowers of *Erythrina leptorhiza*.—A–B. Illegitimate visits by *Diglossa baritula* and hummingbirds of moderate size, respectively; C. *Lampornis clemenciae* visiting the flowers in a legitimate way.

both ovule and pollen grain size. Experimental results indicate self-incompatibility, although two cleistogamic flowers were found in a single population. This suggests that self-incompatibility is not absolute in the population. However, the contribution of cleistogamic flowers to the seed pool is insignificant because of their rarity. Our knowledge of the breeding system is limited, and it needs more research.

Following the nomenclature of Barrows (1976) the visitors of *Erythrina leptorhiza* are categorized as nectar-foraging-perforating robbers, nectar-foraging robbers, and pollinators. *Diglossa baritula* bites holes in the corolla and robs the nectar. Although the total number of foraging visits of this species was not higher than that of the other visitors (19.0% of the total), the high proportion of perforated *E. leptorhiza* flowers indicates that the flower-piercer plays an important role in depleting nectar resources. Two hummingbird species (*Hylocharis leucotis* and *Amazilia beryllina*) are also considered as nectar robbers. These two species account for approximately 70% of the total visits. As described above, these two hummingbirds do not pollinate flowers of *E. leptorhiza*, and it is difficult to account for it. However, it is possible that, due to their moderate size, the approach of these hummingbirds to the flowers becomes easier from the outside of the standard. The smallest hummingbird, *Calothorax lucifer*, commonly seen in the forest never visited *E. leptorhiza*. Finally, although the large hummingbird *Lampornis clemenciae* was the one species that took the nectar in a legitimate way, it was characterized by its low frequency of visits (11.1%). In sum, the nectar robbers represent 89% of the total foraging visits recorded and the effective pollinators only 11.1%.



Bird-pollinated flowers generally produce large quantities of nectar (Grant & Grant, 1968; Faegri & van der Pijl, 1971), and a copious amount of nectar available may favor territoriality (Stiles, 1975). Since *Erythrina leptorhiza* grows in large clumps and shows high synchronism in time of blooming, it appears pre-eminently adapted to pollination by territorial hummingbirds. Linhart (1973) has pointed out that hummingbird territoriality can greatly decrease pollen flow, and this may be disadvantageous to the self-incompatible *E. leptorhiza* clumps. Nevertheless, we have found that the feeding strategy of *Lampornis clemenciae* is traplining. The nectar robbers deplete the nectar resources, and, therefore, the available amount of nectar of a single clump does not satisfy the food requirements of this hummingbird. As a result, *L. clemenciae* does not restrict its visits to the flowers of a single clump owing to the depletion by the robbers of the caloric reward presented in the flowers. Therefore, we must consider that nectar robbers may have a positive effect on the reproduction of this plant species. Observations made on the red clover (Hawkins, 1961), and on *Penstemon kunthii* C. Don (Lyon & Chadek, 1971) also reveal that nectar robbing may not be deleterious.

The relatively high amount of nectar in *Erythrina leptorhiza* (42.5  $\mu$ l per flower) in comparison with other hummingbird-pollinated species of the genus, e.g., *E. coralloides* A. DC. with 9.8  $\mu$ l (Cruden & Toledo, 1977), encourages exploitation by the four bird species that visit it.

The third aspect, relation between number of available flowers and fruit set, may be explained in light of the earlier discussions. The increment of fruit set which is inverse to the number of flowers open (Fig. 1) is explainable if the entire population is self-incompatible. If the number of available flowers is high, the probability of geitonogamous pollinations is high as well, and since a clump of *E. leptorhiza* is a single individual genetically, this pollination is ineffectual. By contrast, if the number of flowers open is minimal, fruit set should be maximized, because at this time the amount of nectar in a given clump is not enough to satiate the pollinator (see Heinrich & Raven, 1972, for discussion). This phenomenon sustains some of the theoretical predictions made by Cruden (1976).

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